

# A cave with remarkably high subterranean diversity in Africa and its significance for biodiversity conservation

Soumia Moutaouakil<sup>1</sup>, Marconi Souza-Silva<sup>2,3</sup>, Lais Furtado Oliveira<sup>2,3</sup>,  
Mohamed Ghamizi<sup>1</sup>, Rodrigo Lopes Ferreira<sup>2,3</sup>

**1** Natural History Museum-Research Center, Cadi Ayyad University, Abdelkrim Al Khattabi Avenue, 40000 Marrakech, Morocco **2** Centro de Estudos em Biologia Subterrânea, Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Campus Universitário, P.O. Box 3037, Lavras CEP 37200-000, Minas Gerais, Brazil **3** Programa de Pós-Graduação em Ecologia Aplicada, Universidade Federal de Lavras, Lavras CEP 37200-000, Minas Gerais, Brazil

**Corresponding authors:** Soumia Moutaouakil (moutaouakil.soumia@gmail.com);  
Marconi Souza-Silva (marconisilva@ufla.br)

---

Academic editor: Lubomír Kováč | Received 14 October 2023 | Accepted 15 October 2024 | Published 1 November 2024

<https://zoobank.org/DD8B436E-6F20-4FC3-9D64-D8CB50625982>

---

**Citation:** Moutaouakil S, Souza-Silva M, Oliveira LF, Ghamizi M, Ferreira RL (2024) A cave with remarkably high subterranean diversity in Africa and its significance for biodiversity conservation. *Subterranean Biology* 50: 1–28. <https://doi.org/10.3897/subtbiol.50.113919>

---

## Abstract

Aziza cave, which is also known as kef Aziza or Tazouguert cave, represents an important and large karstic system that consists of more than 3.5 km of surveyed galleries, standing as the fifth most extensive cave system in Morocco and one of the ten largest in North Africa. This study unveils Aziza cave as an important spot of subterranean diversity in Africa. Here, we provide the first checklist of subterranean fauna in this cave, with 26 taxa, comprising 22 troglobiotic and 4 stygobiotic species. Of this total, eight species still require further confirmation of their status. The richest taxa include Coleoptera (5 species), Araneae (4 species), Entomobryomorpha (3 species), and Isopoda (2 species). However, it is noteworthy that only around 34.6% of the cave-restricted species found in the cave have been formally described to date. Additionally, the biodiversity of large system areas remains to be discovered as these areas need to be further explored. Furthermore, this paper highlights the broader conservation challenges faced by subterranean habitats in Morocco, particularly considering human-induced impacts on these remarkable ecosystems. We aim to draw attention to the crucial ecological role of subterranean environments and their extraordinary biological diversity. By doing so, we aim to inspire increased research and conservation initiatives, not just in this area but across Africa.

## Keywords

Aziza, cave conservation, cave diversity, North-Africa, protection strategies

## Introduction

Subterranean ecosystems play a significant role, serving as crucial freshwater reservoirs on a global scale (Goldscheider et al. 2020). These areas are also home to unique species, some with potential biotechnological applications and others that play important roles in maintaining a healthy environment. Despite their importance, these habitats remain poorly explored in many regions worldwide (Pipan et al. 2020; Sánchez-Fernández et al. 2021; Canedoli et al. 2022). Concealed beneath the surface, subterranean habitats harbor an extraordinary diversity of species that have evolved unique adaptations to survive in darkness, facing challenges posed by oligotrophic conditions and high, constant moisture (Kováč 2018; Pipan et al. 2020). While much remains unknown about these environments, recent studies have revealed caves and other subterranean habitats that are recognized as hotspots of subterranean biodiversity (Culver and Sket 2000; Pipan et al. 2020; Iannella et al. 2021; Ferreira et al. 2023; Pipan and Culver 2024).

Several regions worldwide are renowned for hosting hotspots of subterranean biodiversity (HSB), as evidenced in various studies (Pipan et al. 2020; Culver et al. 2021; Huang et al. 2021; Iliffe et al. 2021; Souza-Silva et al. 2021; Ferreira et al. 2023; Pipan and Culver 2024). Although there is some criticism concerning the cutoff criteria to define a subterranean hotspot (Ferreira et al. 2023), the initial concept proposed by Culver and Sket (2000) encompasses caves or other subterranean habitats that harbor 20 or more cave-restricted species.

Among the most well-known is the Dinaric Karst in Balkan Peninsula, extending through several Balkan countries, which provides a habitat for a rich diversity of cave-dwelling species (Sket et al. 2004). Subterranean hotspot locations have been identified across all continents except Africa and Antarctica. These hotspots span latitudes from 25°S to 45°N, including sites within the tropics, specifically within the seasonal tropics. The Southern Hemisphere contains significantly fewer sites, with none located farther south than 25°S. A concentration of hotspots is observed between 40° and 50°N latitudes, corresponding to the previously described ridge of high cave biodiversity in Europe (Culver et al. 2006; Zagmajster et al. 2018; Pipan and Culver 2024). Additionally, hotspots are nearly absent around the equator (Souza-Silva and Ferreira 2016; Souza-Silva et al. 2021; Ferreira et al. 2023; Pipan and Culver 2024).

However, given the arbitrary cutoff number for defining HSB, it is crucial to identify sites or caves with a remarkable diversity of cave-restricted species, even if their count does not reach the minimal cutoffs. This is important for two reasons: (i) the concept of “high diversity” is often context-dependent, varying with the area where a cave is located, and (ii) new species can be discovered even in well-studied caves, as the subterranean realm extends beyond the accessible macrocaverns. Therefore, identifying and emphasizing caves with a high diversity of cave-restricted fauna holds significant potential for conservation efforts and the establishment of specific

protection policies. The specialized adaptations and limited distributions of several subterranean species render them highly susceptible to habitat loss and degradation. As such, the identification and conservation of these hotspots play a pivotal role in ensuring the long-term survival of this exceptional, significant, and fascinating fauna (Niemiller et al. 2018; Pipan et al. 2020; Sánchez-Fernández et al. 2021; Ferreira et al. 2022).

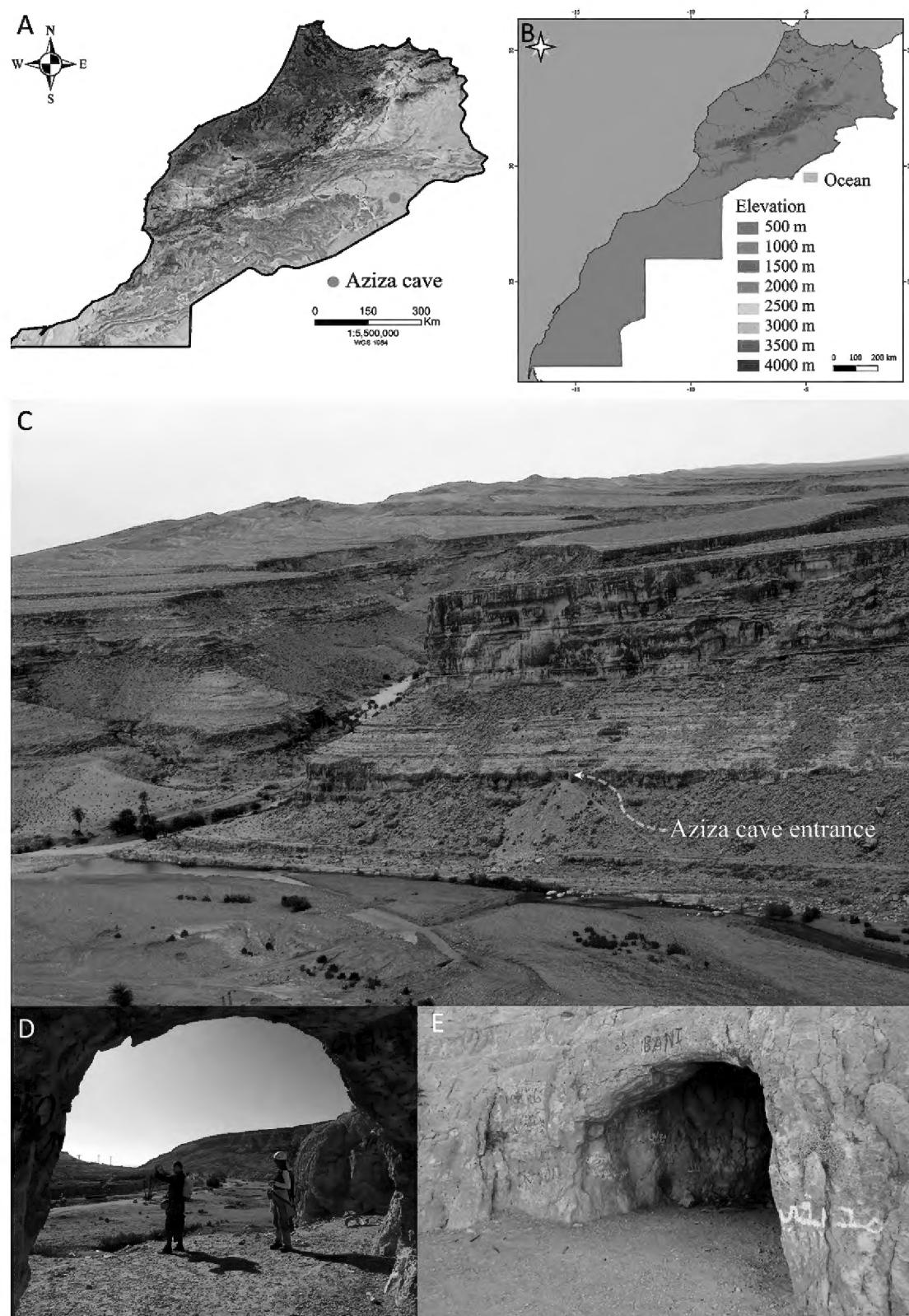
Some areas in Africa have been studied by speleologists (Juberthie and Decu 1994), and a short survey of highly biodiverse cave regions in Africa can be found in Deharveng et al. (2024). Italian zoologists researched Somalia, while Sjöstedt, Al-luaud, and Jeannel explored caves in East Africa (Kenya and Zanzibar). In Congo, Heuts and Leleup explored caves, and Decary, Millot, and Paulian conducted extensive studies in the large caves of Madagascar. Hiernaux and Villiers collected fauna from sandstone and laterite caves in Guinea. Additionally, in North Africa, Peyerimhoff studied subterranean fauna in Algeria, and Strinati and Aellen examined cave fauna in the Taza mountains of Morocco, among others. Furthermore, Leleup worked on a comprehensive review of cave fauna in tropical Africa (Jeannel 1926; Strinati and Aellen 1959; Juberthie and Decu 1994; Vandel 2013). Despite these efforts, significant gaps remain, and African subterranean ecosystems have received little attention from researchers in recent decades. This has made Africa one of the least studied continents regarding cave-restricted species and their associated habitats, likely due to insufficient sampling and the rarity of favorable habitats (Deharveng and Bedos 2018). Despite this lack of attention, previous studies have revealed a diverse array of subterranean species, many of which are found nowhere else on Earth (Hamer and Bredonck 1997; Messana 2004; Messouli 2012; Boutin et al. 2001; Messouli and Boutin 2001; Kayo et al. 2002; Ferreira et al. 2020; Monticelli-Cardoso et al. 2021). The predominant focus of historical research has been on species descriptions, with only a limited number of recent publications delving into cave ecology, community, and conservation (Togouet et al. 2009; Kayo et al. 2012; Vandel et al. 2013; Deharveng and Bedos 2018; Ferreira et al. 2020; Du Preez et al. 2023). These remarkable species are uniquely adapted to thrive in challenging conditions, rendering them particularly intriguing subjects for researchers studying evolutionary biology and biogeography (Trontelj et al. 2012; Culver and Pipan 2019; Pipan et al. 2020; Sánchez-Fernández et al. 2021).

This paper highlights the occurrence of a cave with a remarkable subterranean diversity in Africa, known as the Aziza cave (also referred to as Tazouguert cave and locally as Kef Aziza), located in Morocco. Our study analyzes the cave's distinctive geological and hydrological characteristics and the diverse species inhabiting this unique ecosystem. Additionally, we address the conservation challenges that some subterranean habitats in Morocco face, particularly concerning human-induced impacts on subterranean species. By highlighting these ecosystems and their exceptional biodiversity, we aim to inspire more research and conservation efforts in this region and across Africa.

## Materials and methods

### Study area

The Aziza cave is located in the Tazzouguert Plateau, within the administrative boundaries of the Oued Naam commune near Boudnib town, in the province of Er-Rachidia, within the Drâa Tafilalet region of eastern Morocco (Fig. 1A, B). This cave is in the Moroccan Eastern High Atlas, approximately 80 kilometers from Errachidia town. The area has a population exceeding 92,000 residents (HCP 2019).



**Figure 1.** The location of Aziza cave in Morocco Sahara Desert on a landscape map (**A**) and an altimetric map (**B**). A landscape view of the surrounding area of Aziza Cave (**C**). View from the inside to outside at the entrance (**D**), outside view of the entrance (**E**).

The Aziza cave is situated in a pre-Saharan zone of Morocco (Karmaoui et al. 2022), where approximately 37% of the land area in the province is covered by a stony desert landscape known as ‘Hamadas’. This landscape features an arid environment with hard soil, rock slabs, plateaus, and minimal sand (Fig. 1C). The distribution of rainfall in the Errachidia province is irregular both in time and space, ranging from over 250 mm in the elevated regions, such as the High Atlas, to approximately 130 mm near Errachidia city and dropping to less than 75 mm in the desert areas of the Tafilalet plain (HCP 2018). These significant variations result in hyper-arid climatic conditions within the Tafilalet Basin (Herzog et al. 2021). The temperatures in this region range from -5 °C to 40 °C (Ben Salem et al. 2011).

The area is part of the Guir’s Hamada, a plateau spanning approximately 1000 square kilometers. This plateau is primarily composed of sedimentary layers of Cenomanian-Turonian limestone, consisting of bioclastic limestones with bryozoans and stromatoporidae, followed by marl limestones containing bioclastic ammonites, lamellibranches, echinoderms, gastropods, and bryozoans (Ettachfini et al. 2020).

The Cretaceous sedimentary basin in the region comprises three overlapping exploitable aquifers. Below is an impermeable substratum of Cenomanian Marl (Infracenom), while Senonian sandstones and clay sands are above. Between these layers exists the Turonian, which serves as the primary aquifer in the basin. The thickness of this reservoir varies between 20 and 100 meters. Fissures and karstification of the limestone formations contribute to the formation of several springs, such as Mouy (Qm p 80 l/s), Tamazirt (Qm p 135 l/s), Meski (Qm p 167 l/s), and others, along with the underground network of the Aziza cave, which is classified as hypogenic (El Ouali et al. 1999; Audra 2017).

The province’s economy relies heavily on agriculture, making it highly dependent on water resources. Moreover, the region faces several challenges, including soil and water salinization, desertification, and silting. These challenges exacerbate the region’s vulnerability, underscoring the urgent need for sustainable strategies to mitigate their impacts (Karmaoui et al. 2022). Addressing these issues is crucial to safeguarding the region’s agricultural productivity and ensuring the well-being of its inhabitants.

## Network galleries of Aziza cave

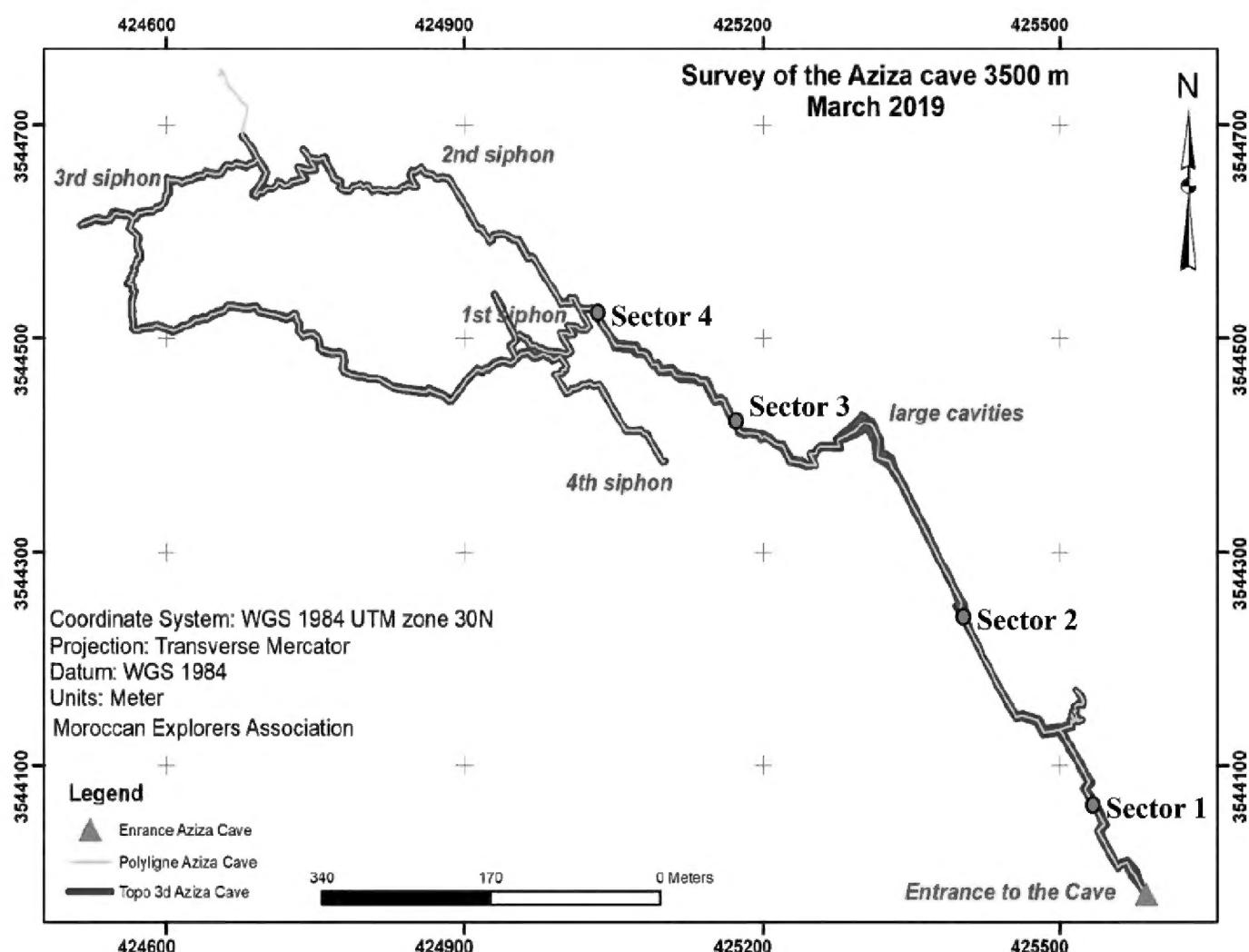
Aziza Cave (32.0146°N, -3.4717°W) is situated in the Eastern High Atlas, approximately 80 kilometers from Errachidia city towards Boudnib, at an elevation of 1059 m above sea level (Benani et al. 2022). The cave is positioned 30 meters above the riverbed on the right bank of the Guir River, within the Turonian limestone formation (Fig. 1C). It boasts two entrances: a horizontal one measuring 2 × 3 m, visible from the road on the river’s opposite side above a scree cone. A few meters away, there is a second entrance, which is vertical (Fig. 1C–E). It is important to note that the cave initially had only a single entrance (the vertical one), and the horizontal entrance was artificially excavated.

The gallery of the cave gently descends, featuring some meanders and detours while maintaining a consistent SE-NW orientation. The first part of the cave features

remarkable and expansive dimensions. After about 450 m from the entrance, one reaches the Guano Room (large cavities in Fig. 2), the largest chamber of the cave, reaching up to 30 m in height. This chamber is home to a colony of hundreds of bats, and on the ground, there are big guano piles, some of which are partially fossilized in ancient areas. Over the subsequent 400 m, the corridor alternates between narrowing and widening, displaying a higher sinuosity coefficient than the first section, resembling a meandering form. The galleries are then continuously divided into two distinct passages that join as tributaries (Branch work cave) (Fig. 2).

## Aziza cave speleogenesis

The location of Aziza Cave near the Guir River suggests that it might have served as an insurgence of the river during periods when the water level was higher than the current cave entrance. However, a study conducted by a Croatian team in 2003 proposed an alternative hypothesis, suggesting that the cave's formation occurred in two distinct stages. The first stage involved a phreatic genesis underground, which was ancient and led to fossilization. During this phase, the slope of the cave might have been lowered due to the erosion caused by the Oued Guir, possibly affecting a part of the cave system. Subsequently, a second phase occurred, which is more recent and primarily affected the deeper parts of the cave through vadose processes. This second phase is



**Figure 2.** Topography of the AZIZA Cave 2019-2020 (Bennani et al. 2022) showing the conduits extension and siphons and sample units (sectors and quadrants) distributions.

not directly linked to the genesis of the main cave system. Instead, it is believed to have evolved in drier climates with well-developed speleogenetic mechanisms, possibly influenced by different lithotypes and favored by widespread absorption on heavily cracked plains of the hamada (Buzio et al. 2003).

The presence of bats has also significantly influenced the cave's morphology. Biogenic corrosion, caused by the secretions of these animals, has had a profound impact on the condition of the cave walls and roofs. The mineralized urine droplets directly attack the surrounding limestone, leading to corrosion over time. Moreover, the combination of ammonia from urine and CO<sub>2</sub> from bats' respiration produces carbonic acid through condensation, further extending the corrosion process. As a result of these physicochemical processes, the main gallery now exhibits various unique features, including ceilings with bell holes, hemispherical domes, and smooth walls, which have erased the original morphologies of the cave (Fig. 3A, B). This chain of erosion processes, driven by bats, their secretions, and the heat they generate, has led to a late enlargement of the cave and the modification of its geometry and characteristics (Dandurand et al. 2019).

## Explorations, topography, and research

The first known explorations of Aziza Cave date back to 1925, followed by another expedition in 1948 (Benani et al. 2022). The Moroccan Caving Society conducted the initial topographical survey of the cave in 1953, resulting in a network development of approximately 1540 meters (up to the first two siphons) with basic estimates of the gallery's height and width (Buzio et al. 2003).

In 1970 a Spanish expedition explored only 1000 meters of the cave (Buzio et al. 2003). Between 1972 and 1979, the cave was partially explored and surveyed, extending the network to around 1500 meters as part of a project funded by the Keimer Foundation in Basel (Buzio et al. 2003). In 1982–1983, various Croatian cave groups discovered a new cave section, adding approximately 960 meters to its total length (Bolanic et al. 1983). In 2003, Italian speleologists conducted a new topographical survey of Aziza Cave, expanding the network to an impressive length of 3500 meters (Buzio et al. 2003). Then, in 2019, a Moroccan team utilized advanced technologies, including Disto X and 3D laser representation, to conduct a topographic survey, revealing a network length of over 4000 meters (Benani et al. 2022) and making it the fifth-largest cave system in Morocco, and one of the 10<sup>th</sup> largest in North Africa (MET 1981; Nehili and Naouadir 2021; Benani et al. 2022).

Aziza cave has been the subject of several biospeological expeditions over the years. The first survey was conducted in 1968 by the Atlas Expedition of "Equip de Recerques Espeleològiques from the Centre Excursionista de Catalunya" (Canals and Viñas 1969; Español 1969). In 1977, a new Atlas expedition was carried out by the "Grup Mediterrània de Barcelona and the Secció d'Investigacions i Recerques Espeleològiques of the Unió Excursionista de Catalunya" (Lagar 1978). In April 1990, an entomological expedition was organized by Catalan members of the



**Figure 3.** The interior of Aziza cave features stunning galleries with bell holes, hemispherical domes, and smooth walls labeled as **A, B, C, E**. Additionally, there are water ponds (**D**).

“Asociación Europea de Coleopterología” (Ribera 1983). Then, in 1997, the cave was visited by the Catalan entomologist Carles Hernando (Barranco and Mayoral 2007). This was followed by an Atlas expedition organized by the Catalan association BIOSP in 2001 (Stüben 2009).

## Literature review on the cave fauna

The data on the Aziza cave fauna was gathered by conducting a comprehensive literature search, focusing on relevant keywords such as “African cave biodiversity,” “Aziza,” “Tazouguert,” “cave fauna,” “troglobitic fauna,” “stygobitic fauna,” “groundwater,” “pollution,” and “North Africa.” We selected the most pertinent databases that contained information related to cave biodiversity.

## Cave climate, organic resources, and physical traits

To investigate the spatial variation of temperature and humidity within the cave, we used temperature and humidity data loggers (accuracy  $\pm 1$  °C for temperature and  $\pm 5\%$  for relative humidity). Starting from the cave entrance, we positioned the instrument on the cave floor and recorded data for 15 minutes (Souza-Silva et al. 2021). Our measurements were taken at eight distinct distances within the cave: 35 meters, 85 meters, 140 meters, 165 meters, 500 meters, and 800 meters from the entrance. In Addition, two temperature measurements were conducted near siphons 1 and 2. We closely monitored the readings until the temperature and humidity levels reached a stable state inside the cave at each point. We also conducted an in-situ examination of the organic resources on the walls and floor of Aziza Cave to gain insights into potential food sources for the fauna. However, we did not quantitatively measure the number of organic resources, their accumulation, access pathways, or decomposition rates. Consequently, our trophic characterization was limited to a qualitative evaluation. Finally, we examined the substrate characteristics of the cave floor to describe the microhabitats available for the fauna.

## Sampling cave invertebrates

to create a comprehensive documentation of invertebrate species to the cave environment, we used various search methods to thoroughly investigate the different microhabitats within the cave (Souza-Silva et al. 2021). Sampling was conducted during multiple cave visits, specifically in 2002, 2003, 2020, and 2022. The survey of invertebrates was conducted utilizing tweezers and brushes using different methods and sampling techniques following the procedures described by Wynne et al. (2019): 1-hand sampling with Direct Intuitive Search (DIS), visual search, and opportunistic collecting. 2-Pitfall trapping. 3-Aquatic substrate sampling. 4-Attractions using bait. Besides this, 12 quadrats (measuring one m<sup>2</sup>) and four sectors (measuring 10 × 3 m) were used to search for small invertebrates within microhabitats during our visit in 2020 (Fig. 2), with the participation of three collectors in the sampling process, and sampling efforts continued until all invertebrates were accounted for. This approach led to a significant increase in the number of cave-restricted species documented in the cave. However, it is important to note that methods involving invertebrate extraction from substrates, such as Berlese-Tullgren funnels, were not employed.

## Determination of troglobionts and stygobionts

The terms stygobionts and troglobionts encompass species that live in caves and various shallow subterranean and above-ground habitats. While most subterranean species typically display troglomorphy, including reduced eyes and pigment, increased size, elongated appendages, and extra-optic sensory structures, certain troglobionts may exhibit limited or no troglomorphy due to factors such as habitat volume, twilight exposure, isolation age, genetic variability, and others. This variability suggests some species may qualify as eutroglophiles (Deharveng et al. 2024). Consequently, uncertain cases have been considered potential troglobionts for terminological consistency, pending further detailed studies to clarify their categorization.

Species restricted to subterranean environments, such as troglobionts and stygobionts, cannot complete their life cycles in aboveground habitats (Sket 2008). One way to identify these subterranean-adapted species is by recognizing specific morphological traits, known as troglomorphisms, commonly observed in troglobitic and stygobitic fauna (Sket 2008; Culver and Pipan 2019). These adaptations include reduced eyes, pigmentation, and hypertrophy of nonvisual sensory structures and locomotor appendages. Such traits provide evidence of the species' adaptation and isolation in subterranean habitats. Many species are easily recognizable as soil species, lacking pigmentation and eyes due to their specialization for life in topsoil and leaf litter. We classified species as "potential troglobionts" if they are exclusively known from Aziza cave and exhibit troglomorphic traits, lacking pigmentation and eyes. However, some species do not display specific adaptations to subterranean life (features inconsistent across all troglobiont species e.g., *Scaurus tingitanus gimeli*). Nevertheless, they were only found within the cave, despite several samplings in external areas and the considerable size of this species. These species were never observed near the entrances, either inside or outside, or at other locations in North Africa more broadly (Chavanon et al. 2015). It is important to note that many specimens of the recently discovered species have not been properly identified and are only classified at higher taxonomic levels. While this lack of taxonomic precision is a limitation, many of these specimens likely represent new taxa. Therefore, as in other instances where species-level identification is not feasible for all taxa (Clark et al. 2021; Deharveng et al. 2021; Ferreira and Souza-Silva 2023; Ferreira et al. 2023), we are presenting the taxa at the highest possible taxonomic level achieved.

While troglomorphisms offer valuable insights into the potential status of species, their analysis must consider the contexts of the external ecosystems surrounding caves (Ferreira and Souza-Silva 2023). For example, suppose a species showing complete depigmentation, blindness, and a reduced cuticle is found in a cave in an arid region. In that case, these morphological traits strongly indicate potential troglobionts. In the surrounding epigean environments, such organisms rarely encounter suitable microhabitats for survival. Hence, considering the epigean desert surrounding the Aziza cave (with temperatures reaching up to 40 °C and air moisture measured on October 6, 2022, of approximately 22.6%), it is unlikely that troglomorphic

species could maintain viable populations on the surface. In contrast, the temperature inside the cave is around 23 °C ( $\pm 1.5$ ), with an air moisture level of about 92.2%. Therefore, troglomorphic traits not only played a crucial role in identifying these species as troglobitic but also the external conditions, which were highly restrictive, imposing physiological constraints and preventing their occurrence in external habitats. All these factors collectively lead us to attribute troglobiont characteristics to these new species.

## Human uses and alterations

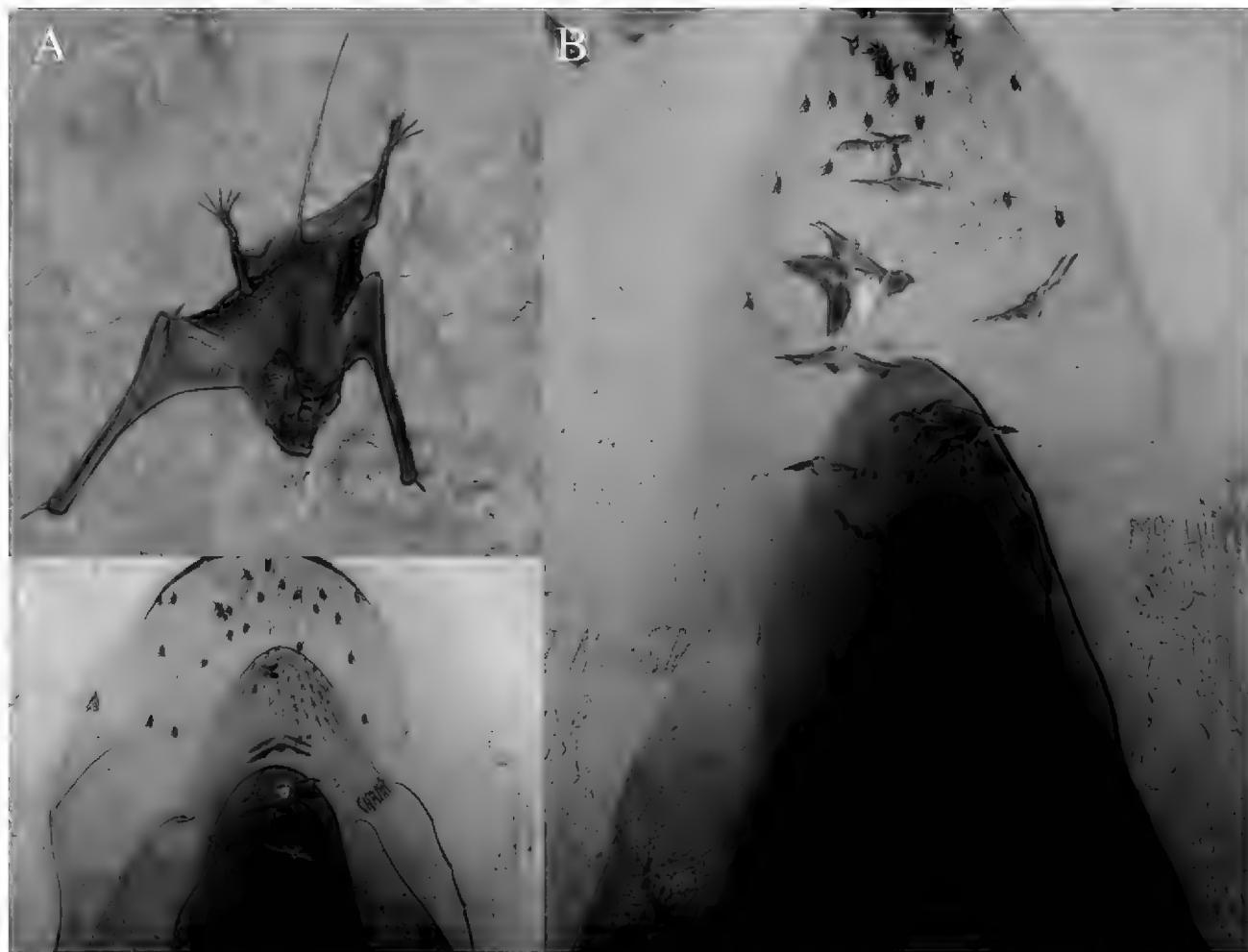
Based on our recent cave explorations and a review of existing literature, we have assessed and categorized human interactions with modifications to the cave and its surrounding areas. Our evaluation, guided by the framework established by Souza-Silva et al. (2015), provides a detailed qualitative account of these impacts. Additionally, one of our researchers, S. Moutaouakil, has visited the cave and its vicinity to identify potential human-induced changes.

## Results

### Cave's climate, microhabitats and organic resources

The cave displayed distinct conditions within its inner regions. Close to the entrance, the air was noticeably dry (up to 80 m – 62.4% moisture content), while deeper inside (after 100–150 m), it became increasingly humid (reaching 98.2% moisture content after 800–850 m), resulting in a diverse and heterogeneous cave ecosystem concerning humidity levels. The average air temperature inside the cave hovered around 23 °C ( $\pm 1.5$ ), with inner portions maintaining an average air moisture of about 80% ( $\pm 18$ ). The cave floor displays organic and inorganic materials such as bat feces, plant debris (from torches used by visitors), and various types of clastic sediments, ranging from large rocks to gravel, sand, silt, mud, and hardpan. This diverse mix of materials allows for different microhabitats with varying characteristics as you move from the cave entrance to its deeper sections. Notably, the substrate composition near the entrance showed more diversity, while it became less varied in the deeper parts of the cave.

The primary sources of nutrients for terrestrial and aquatic fauna within the cave are guano and bat carcasses. Additionally, plant debris is scattered throughout the cave, displaying various degrees of decomposition (Fig. 6A–C). This plant debris appears to have been brought into the cave by sporadic human visitors from external environments. While not serving as a regular food source, the cave-restricted millipede *Jeekelosoma abadi* was observed feeding on both the plant debris (Fig. 6C) and guano pellets (Fig. 6D), demonstrating the generalist diet of this species, which may also be the case of several other cave-restricted detritivores found in this cave.



**Figure 4.** Long-tailed bat *Rhinopoma hardwickei* (**A**), and other bats (**B, C**) were observed inside Aziza cave.

### Bat assemblages and abundance in Aziza cave

In May 2002, the cave hosted several colonies of *Rhinolophus euryale* Blasius, 1853, and *Myotis punicus* Felten, Spitzenberger & Storch, 1977. These bats were mostly found scattered across the ceiling of the large chamber, approximately 450 meters from the cave's entrance (Fig. 4). However, in April 2003, the colonies were significantly smaller, accounting for about one-third of the population observed in 2002. By the winter of 2003, the number of bats further declined, with only approximately two hundred individuals observed, including *Myotis punicus*, *Rhinolophus euryale*, and *Rhinopoma hardwickei* Gray, 1831. The latter species, with a tail almost as long as its body, is generally found in small groups of up to 10 individuals or even solitary (Buzio et al. 2003).

The discovery of some bat corpses enabled species identification through bone measurements, revealing the presence of a fourth species: *Miniopterus schreibersii* (Kuhl, 1817). In 2014, the Aziza cave was designated as the type locality for a new species: *Miniopterus maghrebensis* Puechmaille, Allegrini, Benda, Bilgin, Ibañez & Juste, 2014 (Puechmaille et al. 2014). This discovery increased the diversity of bats in this cave, bringing the total number to five species.

### Cave-restricted fauna

To date, 26 troglobitic and stygobiotic species have been documented within Aziza cave, comprising 22 troglobiotic and 4 stygobiotic species. Of this total, eight species still require further confirmation of their status; thus, at least 18 are cave-restricted. These

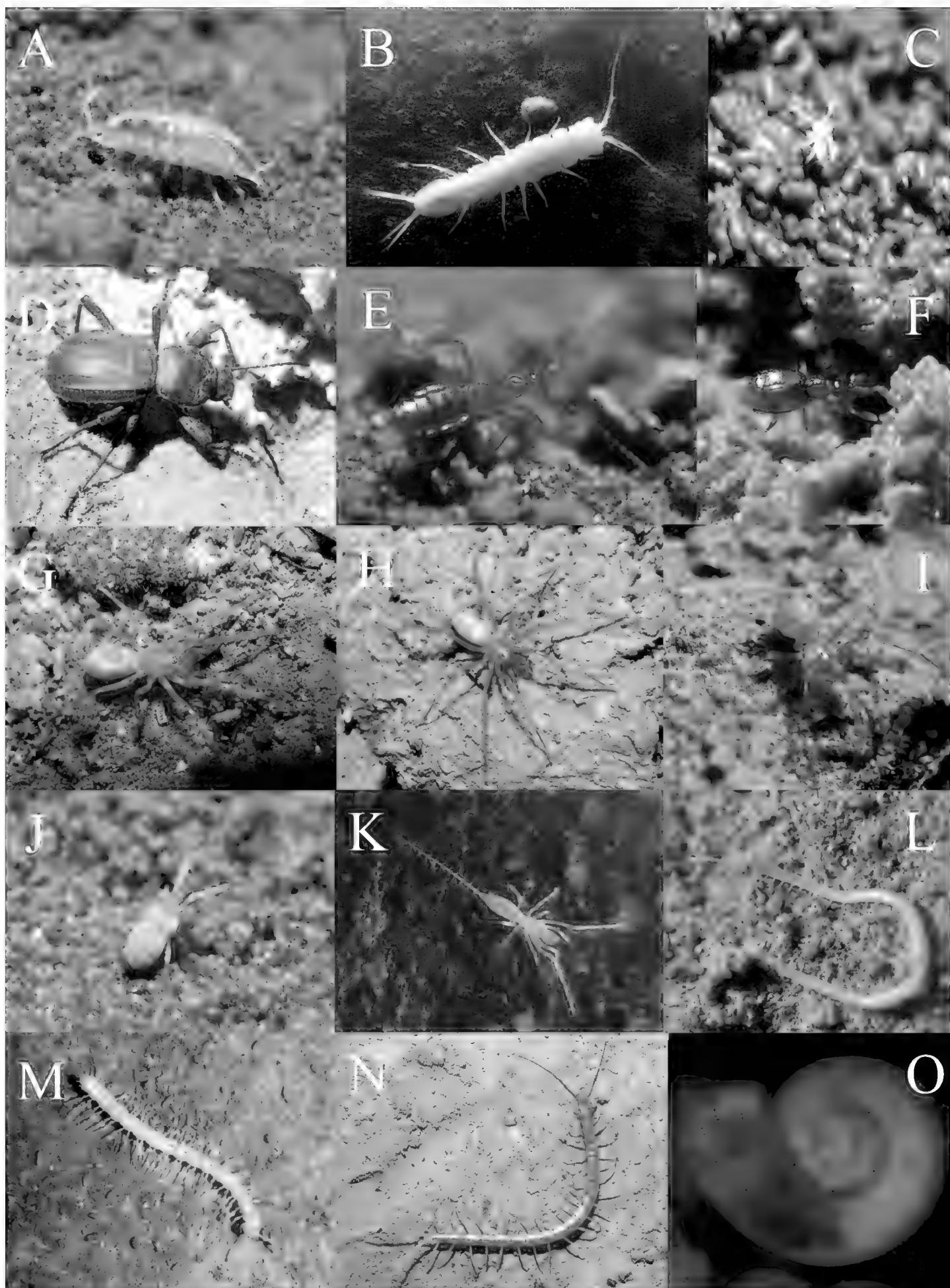
species are distributed across several taxonomic groups: Arachnida (7 species), Insecta (6 species), Crustacea (4 species), Collembola (4 species), Chilopoda (2 species), Gastropoda (2 species), and Diplopoda (1 species) (Table 1). The richest taxa include Coleoptera (5 species), Araneae (4 species), Entomobryomorpha (3 species), and Isopoda (2 species). The remaining taxa, such as Bathynellacea, Copepoda, Eupumonata, Geophilomorpha, Sternorrhyncha, Neotaenioglossa, Palpigradi, Polydesmida, Pseudoscorpiones, Scolopendromorpha, and Symphyleona, are represented by one species each (Fig. 5).

Notably, only around one-third (34.6%) of the cave-restricted species found in the cave have been formally described to date. These described species include *Dysdera caeca* Ribera, 1993, *Leptyphantes fadriquei* Barrientos, 2020, *Eukoenia maroccana* Barranco & Mayoral, 2007, *Platyderus insignitus presaharensis* Lagar Mascaró, 1978, *Torneuma troglodytis* Stüben, 2009, *Apteronillus ruei* Español, 1969 (Perreau and Faille 2012), *Scaurus tingitanus gimeli* Peyerimhoff, 1948, *Jeekelosoma abadi* Mauriès, 1985, *Magnezia gardei* Magniez, 1978.

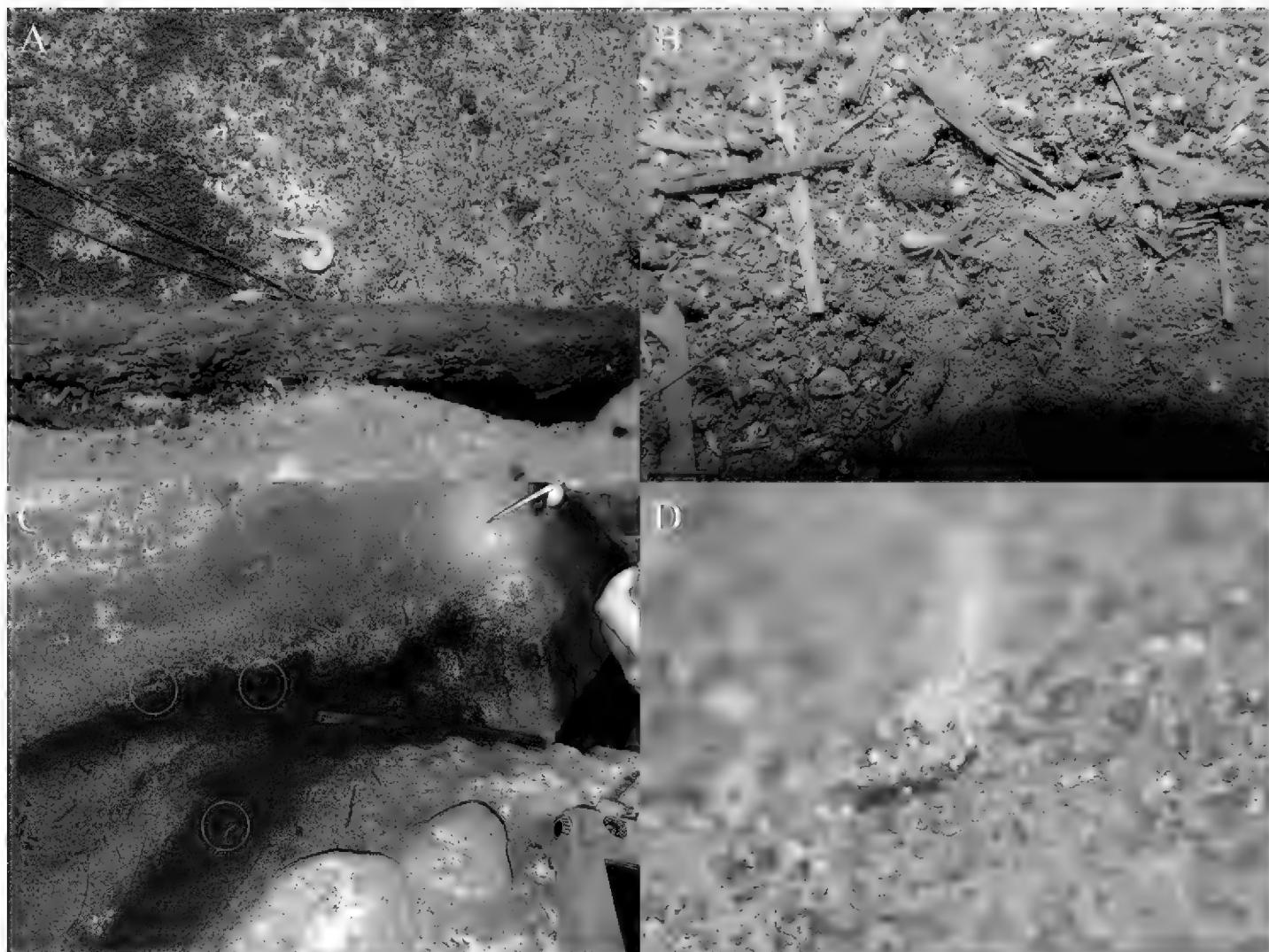
Regarding the aquatic fauna, Aziza Cave has revealed the presence of four stygobiont species: the isopod *Magnezia gardei*, a hydrobiid gastropod, a copepod species,

**Table 1.** The Aziza cave in Er-Rachidia, Morocco, is home to a diverse array of terrestrial and aquatic obligate cave-dwelling invertebrates. Unidentified (un). TB -Troglobite; SB - Stygobite; TB? - Potential troglobionts (further studies needed for confirmation).

TAXON	TAXON	Family name	Species/morphotypes	Status	
Arachnida	Acari	Parasitengona	Parasitengona sp. 1	TB?	
	Araneae	Hahniidae	Hahniidae	TB	
		Dysderidae	<i>Dysdera</i> sp.	TB	
		Linyphiidae	<i>Dysdera caeca</i> Ribera, 1993	TB	
	Palpigradi	Eukoeneniidae	<i>Leptyphantes fadriquei</i> Barrientos, 2020	TB	
		Chthoniidae	<i>Eukoenia maroccana</i> Barranco an Mayoral, 2007	TB	
	Pseudoscorpiones	Chthoniidae	<i>Chthoniidae</i> sp.	TB?	
	Collembola	Symplypleona	<i>Arrhopalites</i> sp.	TB?	
		Entomobryomorpha	un	Entomobryidae sp. 1	TB?
			un	Entomobryidae sp. 2	TB?
			un	Isotomidae sp. 1	TB?
Insecta	Coleoptera	Carabidae	<i>Platyderus insignitus presaharensis</i> Lagar Mascaró, 1978	TB	
		Curculionidae	<i>Torneuma troglodytis</i> Stüben, 2009	TB	
		Pselaphinae	<i>Tychobythinus</i> sp.	TB?	
		Staphylinidae	<i>Apteronillus ruei</i> Español, 1969	TB	
		Tenebrionidae	<i>Scaurus tingitanus gimeli</i> Peyerimhoff, 1948	TB	
		Kinnaridae	<i>Kinnaridae</i> sp.	TB	
Diplopoda	Polydesmida	Paradoxosomatidae	<i>Jeekelosoma abadi</i> Mauriès, 1985	TB	
Chilopoda	Scolopendromorpha	Cryptopidae	<i>Cryptops (T.) aff. numidicus aelleni</i> Manfredi, 1956	TB?	
	Geophilomorpha	un	Geophilomorpha sp.	TB?	
Crustacea	Bathynellacea	Bathynellaceae	Bathynellaceae sp.	SB	
	Isopoda	Ollibrinidae	<i>Castellanethes</i> sp.	TB	
	Asellota	Stenasellidae	<i>Magnezia gardei</i> Magniez, 1978	SB	
	Copepoda	un	Copepoda sp.	SB	
Gastropoda	Eupumonata	un	Eupulmonata sp.	TB?	
	Neotaenioglossa	Hydrobiidae	Hydrobiidae sp.	SB	



**Figure 5.** Some of the species restricted to the Aziza cave, Morocco. *Castellanethes* sp. 1 (**A**), *Magnezia gardei* (**B**), *Arrhopalites* sp. 3 (**C**), *Scaurus tingitanus gimeli* (**D**), *Apteranillus ruei* (**E**), *Tychobythinus* sp. (**F**), *Dysdera* sp. 1 (**G**), *Dysdera caeca* (**H**), *Lepthyphantes fadriquei* (**I**), *Parasitengona* sp. 1 (**J**), *Eukoenenia marociana* (**K**), *Geophilomorpha* sp. 1 (**L**), *Jeekelosoma abadi* (**M**), *Cryptops (Trigonocryptops)* aff. *numidicus aelleni* (**N**), *Eupumonata* sp. 24 (**O**).



**Figure 6.** In Aziza Cave, terrestrial invertebrates rely on plant debris (**A, B, C**) and small guano pellets (**D**) as sources of nutrients. Specimens of *J. abadi* forage on plant debris for sustenance, indicated by red circles in section **C**. Additionally, the red arrow in section **D** highlights the presence of *J. abadi* specimens foraging on guano pellets.

and a Bathynellacea species. The first two species are found in a small, clayey substrate puddle 4 meters in length and 1 meter in depth, located in the left branch 1000 meters from the entrance (Figs 2, 3D) (water temperature: 22.44 °C; conductivity: 506 µS/cm). The copepod and Bathynellacea were found in a large lake on the right branch after the second siphon (Fig. 2) (water temperature: 22.5 °C; conductivity: 348 µS/cm).

*Magniezia gardei* was first described from Aziza Cave but has a relatively broad distribution, having been found in several wells in the Errachidia and Zagora regions (Ait Boughrous et al. 2007; Boudellah et al. 2022). The stygobiotic gastropod is a new species of a new genus currently under description (M. Ghamizi, pers. comm.).

The terrestrial fauna in Aziza Cave exhibits remarkable diversity, comprising 22 troglobitic and/or troglomorphic species (Table 1). Species classified as troglomorphic exhibit adaptations and characteristics indicative of specialization in subterranean environments. For example, the spider Hahniidae displays pale coloration and is eyeless, while the pseudoscorpion Chthoniidae has a pale-yellow color and lacks eyes or eye spots. *Scaurus tingitanus gimeli*, with its elongated legs and antennae, differs from the

typical form found in epigean populations in northern Morocco (Labrique 1995; Vinnolas and Maso 2005).

Regarding their sampling areas, Hahniidae sp. were observed 400 meters from the entrance, while the Coleoptera *Scaurus tingitanus gimeli* is distributed between 200 meters and 800 meters. Because the species is only known from caves and appears absent on the surface (assuming adequate sampling in the area), it is justifiable to categorize it as a troglobiont, regardless of the Labrique (1995) statement, which considered the species as troglophile, even assuming its restriction to the cave environment.

A solitary individual of Chthoniidae sp. was captured 600 meters from the entrance, near the remains of a mammal (sheep or goat bones were observed).

Several species are endemic to this cave, including the Diplopoda *Jeekelosoma abadi*, the Araneae *Dysdera caeca* and *Lepthyphantes fadriquei*, and the Palpigradi *Eukoenenia maroccana*. These species are distributed in the explored part of the cave beyond the guano room, a large cavity depicted in Fig. 2. Additionally, the Coleoptera *Apteranillus ruei* and *Torneuma troglodytis* were captured in narrow galleries after 800 meters from the entrance. The coleopteran *Platyderus insignitus presaharensis* was 200 meters from the entrance (Espanol 1969; Mascaro 1978; Barranco and Mayoral 2007; Stüben 2009; Barrientos 2020).

The coleopteran Pselaphinae *Tychobythinus* sp., the Sternorrhyncha Kinnaridae sp., and the Geophilomorpha sp. were collected in clayey habitats with humidity levels close to saturation (over 98%) after 800 meters from the entrance. The species of Kinnaridae was collected near the third siphon.

## Human use and alterations

In addition to its proximity to a town (Boudnib, 19.7 km), the cave is situated near a paved road (Fig. 7A), making it easily accessible to visitors. The cave entrance currently lacks a gate, allowing unrestricted access. In addition, there are ongoing activities in the riverbed directly in front of the cave entrance, involving the use of tractors to extract gravel (Fig. 7A, B).

The initial section of the cave, easily accessible to visitors, has unfortunately been heavily impacted by graffiti and trampling. As one approaches the entrance, litter and shattered rocks, along with fragments of glass and plastic, can be observed (Fig. 7C). Various drawings and writings have marred the once pristine white walls of the cave, created using mud, paint, or charcoal (Fig. 7D–G). Moreover, remnants of ash, burned pieces of wood, and fragments of broken glass can be found inside the cave. The local inhabitants, possibly fearing respiratory diseases caused by guano (such as histoplasmosis), may have attempted to remove the animals by using numerous wind torches placed in the walls around the large chamber (Moutaouakil S. Personal communication). These activities potentially threaten the cave environment and its delicate ecosystem.



**Figure 7.** Human activities have significantly impacted the Aziza caves and their surrounding area. The construction of roads and using tractors near the riverbed have affected the caves directly, particularly entrances **(A, B)**. Additionally, the caves have been marred by the deposition of garbage at entrance **C** and graffiti along the cave walls at positions **D, E, F, G**.

## Discussion

The Aziza Cave stands out as a significant subterranean habitat, presenting 18 troglobiotic and stygobiotic species, plus eight taxa that may also represent cave-restricted species, making it the richest cave regarding troglofauna and stygofauna in Africa. The second richest cave is the Wynberg Cave System, located in the mountains of Cape Town, South Africa, which hosts 19 cave-restricted species (Ferreira et al. 2021). It is worth mentioning that although the Wynberg Cave System has not been officially proposed as a subterranean biodiversity hotspot, it indeed represents a hotspot in the African continent, based on criteria proposed by Souza-Silva et al. (2015) and Ferreira et al. (2023). According to these authors, the Wynberg Cave System should be considered a hotspot of subterranean biodiversity due to its significant richness of cave-restricted species, considering both its siliciclastic lithology, which typically harbors fewer species of this category, and the increasing anthropogenic impacts it faces. Therefore, both Aziza and the caves from the Wynberg Cave System deserve the utmost attention in terms of protection and conservation policies.

### Subterranean biodiversity of Aziza cave

The high number of cave-restricted species in Aziza Cave can be attributed to a combination of factors. Firstly, its location in the Sahara Desert gives this cave a unique setting, distinguishing it from the arid and harsh surface environment. The high and constant humidity conditions within the cave starkly contrast with the arid surroundings. The species richness may also be linked to historical climatic changes in the region where the cave is situated (Jeannel 1943; Magniez 1978; Huges et al. 2018).

Furthermore, the substantial size of the cave, stretching approximately 4 kilometers, provides ample space for the development of several microhabitats, which can support various distinct invertebrate taxa. Lastly, the presence of subterranean water bodies further enhances the diversity of terrestrial and aquatic habitats available for colonization by the fauna. It is important to mention that a high richness of cave-restricted species is often associated with large subterranean spaces, high productivity, and/or isolated water bodies separate from the surface (Culver and Pipan 2009). These factors collectively contribute to the remarkable biodiversity observed in Aziza Cave.

The distribution and degree of adaptation of most cave-dwelling invertebrates within caves are often more influenced by the physical environment of the cave rather than by food resources or cave geology (Novack et al. 2012; Pacheco et al. 2020; Nicolosi 2021; Souza-Silva et al. 2021; Furtado-Oliveira et al. 2022). Obligate cave-dwelling invertebrates typically have their distribution determined by humidity conditions, thriving in places with stagnant air that is saturated with water vapor. However, many species also venture into the transition zone, either in search of food or inadvertently (Howarth 1988; Humphrey 1990; Wilkens et al. 2000; Souza-Silva and Ferreira 2016; Souza-Silva et al. 2021; Souza and Ferreira 2022).

## Sampling effort and the “lack” of Subterranean Biodiversity Hotspots in Africa

The apparent scarcity of Subterranean Biodiversity Hotspots in Africa is a noteworthy issue. Despite the continent’s vast expanse and its potential for hosting unique subterranean ecosystems, there has been limited exploration and documentation of these habitats. This dearth of attention to subterranean biodiversity has led to significant knowledge gaps, impeding our understanding of the richness and ecological importance of these ecosystems in most parts of the continent.

While the biodiversity of Aziza Cave has been extensively documented, it is important to highlight that the current fauna list is likely incomplete. There are still unexplored areas within the cave that necessitate comprehensive biological inventories. Furthermore, many microhabitats have not been adequately sampled, as specific techniques for sampling smaller invertebrates in terrestrial and aquatic habitats were not employed, as mentioned in the methodology.

We must not assume that the species richness of a subterranean habitat is fully known, which is why new explorations are often necessary (Souza-Silva and Ferreira 2016; Culver et al. 2021; Ferreira and Souza-Silva 2023). Sampling subterranean environments poses challenges due to the inaccessibility of fissures, interstitial habitats, and caves (Culver and Pipan 2009; Trontelj et al. 2012; Ortunó et al. 2013; Mamola et al. 2021; Ferreira et al. 2023). It is important to conduct multiple collections to accurately document the diverse range of life in subterranean habitats. However, for comparative studies, rapid assessment methods can be used with success (Simões et al. 2015; Souza-Silva et al. 2015), if a standardized sampling approach is employed. In situations like these, caves with many troglobiotic species are expected to stand out even with minimal collection efforts (Souza-Silva and Ferreira 2016). The historical absence of biodiversity hotspots in Africa’s subterranean regions can be attributed to the lack of comprehensive studies on this continent. Additionally, the absence of standardized sampling methods may have hindered the identification of areas requiring conservation attention (Souza-Silva and Ferreira 2016; Culver et al. 2021; Ferreira et al. 2023).

On the other hand, according to Culver et al. (2021), the latitudinal distribution of subterranean biodiversity hotspots exhibits a bimodal pattern. Most of these sites are predominantly situated in temperate zones, typically between 40 and 50 degrees north or south of the equator. Particularly for the northern hemisphere, this latitude corresponds to the region traditionally regarded as having the highest richness of subterranean species, a pattern often attributed to the effects of repeated Pleistocene glaciations (Jeannel 1943). A second region is represented by subtropical and sub-temperate areas, approximately 20 and 30 degrees north and south of the equator. These locations mainly consist of lava tubes and wells connected to chemoautotrophic zones. Interestingly, none of these sites are in arid tropics, suggesting that food availability and maintaining high moisture content may also be significant factors influencing species richness (Culver et al. 2021).

## Conservation and protection of Aziza cave fauna

Conserving the fauna of Aziza Cave presents a significant challenge, as it is impacted not only by local factors but also by local and global climate issues (Akdim 2015; Boudellah et al. 2022; Karmaoui et al. 2022).

Aziza Cave is situated within the UNESCO Biosphere Reserve, Oasis du Tafilalet (Ramsar site no. 1483), a site of significant biological and ecological importance. Oasis du Tafilalet is in Errachidia, Goulmima, Sahara SE Morocco ( $31^{\circ}17'N$ ,  $004^{\circ}15'W$ ), covering an area of approximately  $1,370\text{ km}^2$ . The site encompasses a series of oases, serving as the reservoir for one of Morocco's oldest dams, Hassan Ad-Dakhil, which contains small rivers, irrigation channels, and lagoon areas. It serves as an essential wintering ground for migratory birds and is home to notable populations of Rüppell's pipistrelle bat (*Pipistrellus rueppelli*). Agriculture is a prominent activity in the region, with Alfalfa, cereals, henna, date palms, and fruit trees being the primary crops. Sheep farming is also prevalent.

However, the management of dam water releases downstream has resulted in some channels having water only during specific times of the year, further exacerbated by excessive water abstraction for agriculture and human consumption, along with the increased frequency of droughts in recent decades. Additionally, soil salinization has become a problem in various areas due to high evaporation rates (Ait Boughrous et al. 2007; Messouli et al. 2008; <https://rsis.ramsar.org/ris/1483>). These chemical differences in water dripping from epikarst can affect certain communities' persistence (e.g., copepods) (Pipan 2004; Pipan et al. 2006; Culver and Pipan 2010).

Subterranean habitats, such as caves, are relatively unexplored environments with limited attention due to their challenging accessibility (Mammola et al. 2021). Cave environments' extreme isolation and distinct conditions render many species rare and vulnerable. Numerous obligate cave-dwelling species are deemed threatened or endangered at regional or global scales, primarily due to their confinement to small geographical areas (Culver and Pipan 2019).

When Culver and Sket (2000) classified subterranean biodiversity hotspots, they overlooked the degree of threat these habitats faced, neglecting the hotspot model proposed by Myers et al. (2000) for surface environments. Areas susceptible to economic activities undergo rapid landscape transformations, and in many cases, these changes are irreversible. Previously well-conserved landscapes can be swiftly altered into grazing areas or devastated by mining activities (Souza-Silva et al. 2015; Souza-Silva et al. 2021; Ferreira et al. 2023).

In this context, relying solely on the richness of troglobiotic species may not accurately reflect the "health" of a specific subterranean system, as this will depend on the type of impact it has endured (Souza-Silva et al. 2015; Ferreira et al. 2023). Therefore, the degree of impact to which a cave is subjected should be incorporated into this concept (Ferreira et al. 2023), especially considering that conservation policies often prioritize investments. Regrettably, numerous caves are being damaged or experiencing adverse impacts due to unsustainable tourism, overcrowding, and acts of vandalism, jeopardizing their integrity and ecological value (Culver et al. 2021; Nanni et al. 2023).

Numerous conservation efforts have been undertaken worldwide to safeguard subterranean habitats, their fauna, and the ecosystem services they provide. A comprehensive global assessment, drawing from the opinions of over 150 experts, has identified that legislation, public policies, landscape protection and management, and environmental education constitute the most crucial conservation measures (Nanni et al. 2023). In the context of Aziza Cave, implementing these conservation measures is imperative to ensure the protection of its endemic cave-dwelling invertebrates and the preservation of its unique ecosystem services.

Conservation based on establishing legally protected areas and their proper management has been widely recognized as one of the most effective strategies to combat biodiversity loss in various ecosystems (Maxwell et al. 2020). Protecting large areas has proven effective, particularly in cases where little is known about the true extent of the habitat to be preserved and the ecology of the species present, as often seen in subterranean ecosystems (Nanni et al. 2023). However, the effectiveness of these strategies is not absolute, and all sites continue to face threats to some degree. In addition, there is a tangible risk of conflicts if legislation regarding subterranean environments is imposed, as demonstrated by the challenges faced protecting karsts in the Philippines (Urich et al. 2001). Therefore, it is not feasible to rely on a single model to reduce threats and protect subterranean biodiversity spots. Each situation must be carefully considered individually, especially during threat assessments. The threat levels serve as the fundamental criteria for devising appropriate protective measures. However, it is essential to recognize that all global subterranean biodiversity hotspots are worth protecting and serve as valuable sources of regional and national heritage information (Culver et al. 2021). In Morocco, we posit that engaging the local population, when they are cognizant of the significance of these ecosystems and integrated into the implemented projects, will be a crucial foundation for the long-term protection of the cave. The law on Protected Areas (22/07) can be employed to safeguard these sites through a participatory approach.

Promoting awareness campaigns, adopting responsible practices, and embracing sustainable approaches must be the focal point of our conservation endeavors, particularly in the case of Aziza Cave, which harbors such diversity of cave-dwelling invertebrates. Cultivating deep respect for these fragile environments among the local population and implementing effective conservation strategies are paramount. Through these endeavors, we can ensure the enduring survival and safeguarding of these subterranean treasures for the benefit of future generations (Souza-Silva et al. 2019; Gavish-Regev et al. 2023).

Finally, addressing these challenges requires concerted efforts to increase sampling and exploration activities in African caves and other subterranean environments. By focusing on areas with high potential for cave-restricted species, researchers can contribute to identifying and designating new Subterranean Biodiversity Hotspots on the continent. These designated hotspots will serve as focal points for conservation and research initiatives, allowing us to protect better and comprehend the unique life forms that thrive in these underground realms.

## Acknowledgments

Laís Furtado Oliveira was sponsored by Capes Foundation (Coordination for the Improvement of Higher Education Personnel) with 48 months of scholarships. Rodrigo Lopes Ferreira thanks the National Council for Technological Development and Scientific Development (CNPq) for research grant nº 302925/2022-8. We are thankful to Guilherme Prado (Pseudoscorpiones), Giovanna Monticelli Cardoso (Isopods), Leopoldo Bernardi (Acari), and Sylvain Lecigne (Araneae) for their help in identifying the fauna. We thank VALE/SA for financial support. A special thanks to Abderrahim S'khifa and Jean-Philippe Degletagne for their assistance in the fieldwork

## References

- Ait Boughrous A, Yacoubi Khebiza M, Boulanouar M, Boutin C, Messana G (2007) Groundwater quality in two arid areas of Morocco: impact of pollution on biodiversity and paleogeographic implications. *Environmental technology* 28(11): 1299–1315. <https://doi.org/10.1080/09593332808618887>
- Akdim B (2015) Karst landscape and hydrology in Morocco: research trends and perspectives. *Environmental Earth Sciences* 74(1): 251–265. <https://doi.org/10.1007/s12665-015-4254-5>
- Barranco P, Mayoral JG (2007) A new species of *Eukoenenia* (Palpigradi, Eukoeneniidae) from Morocco. *The Journal of Arachnology* 35(2): 318–324. <https://doi.org/10.1636/H05-23.1>
- Barrientos JA, Brañas N, Mederos J (2020) The high complexity of Micronetinae Hull, 1920 (Araneae, Linyphiidae) evidenced through ten new cave-dweller species from the Morocco. *Zoosystema* 42(1): 1–29. <https://doi.org/10.5252/zoosystema2020v42a1>
- Ben Salem A, Messouli M, Yacoubi-Khebiza M (2011) Developing na oasis-based water management tool: Ecohydrologic approach and weap software for a large arid catchment in Morocco. *International Journal of Water Resources. Arid Environ* 1(6): 387–396.
- Benani H, Ouzzaouit, LM, Boudad L, Rhinane H, Nehili A, El Khalki Y, Slimani N (2022) Topographic Survey with Disto x and 3D Representation of the Caves by Laser Grammetry, Case of the Aziza Cave, Errachidia, Morocco. *The Iraqi Geological Journal* 55: 21–34. <https://doi.org/10.46717/igj.55.1D.2Ms-2022-04-18>
- Boudellah A, El Moustaine R, Maliki A, Moutaouakil S, El Gharmali A, Boulanouar M, Ghamizi M (2022) Impacts of Anthropogenic Factors on the Groundwater Ecosystem of Fezouata in South-East of Morocco. *Journal of Ecological Engineering* 23(5).
- Boutin C, Decou V, Juberthie C, Besson JP, Messouli M (2001) Maroc. In: Juberthie C, Decou V (Eds) *Encyclopaedia Biospeologica*, Vol. 3, Intern. Soc. Biospeleol. publ., Moulis (France) and Bucarest (Romania), 643–651.
- Buzio A, Cantaluppi G, De Blasi M, Guffanti M, Repetto G (2003) Kef Aziza, la lunga storia di una grotta pre-sahariana. *Speleologia* 49: 74–78
- Camacho AI, Puch C (2021) Ojo Guareña, A hotspot of subterranean biodiversity in Spain. *Diversity* 13: 199. <https://doi.org/10.3390/d13050199>

- Canedoli C, Ficetola GF, Corengia D, Tognini P, Ferrario A, Padoa-Schioppa E (2022) Integrating landscape ecology and the assessment of ecosystem services in the study of karst areas. *Landscape Ecology* 37: 347–365. <https://doi.org/10.1007/s10980-021-01351-2>
- Chavanon G, Daoudi L, Labrique H (2015) Contribution à la connaissance des coléoptères de la région de Beni Tadjite-Talsint (Maroc Oriental) (Carabidae, Scarabaeoidea, Dermestidae, Buprestidae, Tenebrionidae et Curculionidae). *Bulletin de la Société entomologique de Mulhouse* 71(2): 19–28
- Clark HL, Buzatto BA, Halse SA (2021) A hotspot of arid zone subterranean biodiversity: The Robe Valley in Western Australia. *Diversity* 13(10): 482. <https://doi.org/10.3390/d13100482>
- Culver DC, Deharveng L, Pipan T, Bedos A (2021) An Overview of Subterranean Biodiversity Hotspots. *Diversity* 13: 487.
- Culver DC, Pipan T (2019) *The Biology of Caves and Other Subterranean Habitats*; Oxford University Press: Oxford, UK, [ISBN 978-0-19-882076-5]. <https://doi.org/10.1093/oso/9780198820765.001.0001>
- Culver DC, Pipan T (2010) Climate, abiotic factors, and the evolution of subterranean life klima, abiotiski dejavniki in evolucija podzemelskega življenja. *Acta Carsologica* 39(3): 577–586. <https://doi.org/10.3986/ac.v39i3.85>
- Culver DC, Sket B (2000) Hotspots of subterranean biodiversity in caves and wells. *Journal of cave and Karst studies* 62(1): 11–17.
- Culver DC, Deharveng L, Bedos A, Lewis JJ, Madden M, Reddell JR, Sket B, Trontelj P, White D (2006) The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography* 29(1): 120–128. <https://doi.org/10.1111/j.2005.0906-7590.04435.x>
- Dandurand G, Duranthon F, Jarry M, Stratford DJ, Bruxelles L (2019) Biogenic corrosion caused by bats in Drotsky's Cave (the Gcwihaba Hills, NW Botswana). *Geomorphology* 327: 284–296. <https://doi.org/10.1016/j.geomorph.2018.10.027>
- Deharveng L, Bedos A (2018) Diversity of Terrestrial Invertebrates in Subterranean Habitats. In: Moldovan O, Kováč L, Halse S (Eds) *Cave Ecology. Ecological Studies*, Vol. 235. Springer, Cham. [https://doi.org/10.1007/978-3-319-98852-8\\_7](https://doi.org/10.1007/978-3-319-98852-8_7)
- Deharveng L, Rahmadi C, Suhardjono YR, Bedos A (2021) The Towakkalak System, a hotspot of subterranean biodiversity in Sulawesi, Indonesia. *Diversity* 13(8): 392. <https://doi.org/10.3390/d13080392>
- Deharveng L, Bedos A, Pipan T, Culver DC (2024) Global Subterranean Biodiversity: A Unique Pattern. *Diversity* 16: 157. <https://doi.org/10.3390/d16030157>
- Español F (1969) Un nuevo *Apteronillus* cavernícola de la región de Boudenib, Marruecos pre-sahariano (Col. Staphylinidae). *Annales de Spéléologie* 24(1): 171–176.
- Ferreira RL, Bernard E, da Cruz Júnior FW, Piló LB, Calux A, Souza-Silva M, Frick WF (2020) Brazilian cave heritage under siege. *Science* 375(6586): 1238–1239. <https://doi.org/10.1126/science.abb1973>
- Ferreira RL, Berbert-Born M, Souza-Silva M (2023) The Água Clara cave system in Northeastern Brazil: The richest hotspot of subterranean biodiversity in South America. *Diversity* 15: 761. <https://doi.org/10.3390/d15060761>

- Ferreira RL, Giribet G, Du Preez G, Ventouras O, Janion C, Souza-Silva M (2020) The Wynberg cave system, the most importante site for cave fauna in South Africa at risk. *Subterranean Biology* 36: 73–81. <https://doi.org/10.3897/subtbiol.36.60162>
- Ferreira RL, Souza-Silva M (2023) Beyond Expectations: Recent Discovery of New Cave-Restricted Species Elevates the Água Clara Cave System to the Richest Hotspot of Subterranean Biodiversity in the Neotropics. *Diversity* 15(12): 1215. <https://doi.org/10.3390/d15121215>
- Furtado Oliveira L, Ferreira, RL, Rodriguez Fernández JI, Souza-Silva M (2022) Recreational caving impacts of visitors in a high-altitude cave in Bolivian Andes: Main effects on microhabitat structure and faunal distribution. *International Journal of Speleology* 51(2): 93–103. <https://doi.org/10.5038/1827-806X.51.2.2418>
- Gavish-Regev E, Frumkin A, Na'aman I, Langford B, Aharon S, Ya'aran S, Mammola S (2023) The power of academic and public opinion in conservation: The case of Ayyalon Cave, Israel. *Integrative Conservation* 2: 73–79. <https://doi.org/10.1002/inc3.20>
- Goldscheider N, Chen Z, Auler AS, Bakalowicz M, Broda S, Drew D, Veni G (2020) Global distribution of carbonate rocks and karst water resources. *Hydrogeology Journal* 28: 1661–1677. <https://doi.org/10.1007/s10040-020-02139-5>
- Hamer ML, Brendonck L (1997) Distribution, diversity and conservation of Anostraca (Crustacea: Branchiopoda) in southern Africa. *Studies on Large Branchiopod Biology and Conservation*, 12 pp. [https://doi.org/10.1007/978-94-017-3177-5\\_1](https://doi.org/10.1007/978-94-017-3177-5_1)
- HCP [Haut-Commissariat au Plan] (2018) Regional monography of 2016. Royaume du Maroc: High Commission for Planning. Direction Regionale de Draa-Tafilalet 149.
- HCP [Haut-Commissariat au Plan] (2019) Monographie de la province d'Errachidia. Royaume du Maroc: High Commission for Planning. Direction Regionale de Draa-Tafilalet 101.
- Herzog M, Henselowsky F, Bubenzer O (2021) Geomorphology of the Tafilalt Basin, South-East Morocco—implications for fluvial-aeolian dynamics and wind regimes. *Journal of Maps* 17(2): 682–689. <https://doi.org/10.1080/17445647.2021.1990805>
- Howarth FG (1988) Environmental ecology of north Queensland caves: or why are there so many troglobites in Australia. In *Preprints of Papers for the 17<sup>th</sup> Biennial Conference, Australian Speleological Federation Tropiccon Conference, Lake Tinaroo, Far North Queensland*. (L. Pearson, ed.). Australian Speleological Federation, Cairns, Australia, 76–84.
- Huang S, Wei, G, Wang H, Liu W, Bedos A, Deharveng L, Tian M (2021) Ganxiao Dong: A hotspot of cave biodiversity in northern Guangxi, China. *Diversity* 13(8): 355. <https://doi.org/10.3390/d13080355>
- Hughes PD, Fink D, Rodés Á, Fenton CR, Fujioka T (2018) Timing of Pleistocene glaciations in the High Atlas, Morocco: New  $^{10}\text{Be}$  and  $^{36}\text{Cl}$  exposure ages. *Quaternary Science Reviews* 180: 193–213. <https://doi.org/10.1016/j.quascirev.2017.11.015>
- Humphreys WF (1990) The biology of a troglobitic schizomid (Chelicerata: Arachnida) from caves in the semi-arid Cape Range, Western Australia. *Acta Zoologica Fennica* 190: 181–186.
- Iannella M, Fiasca B, Di Lorenzo T, Di Cicco M, Biondi M, Mammola S, Galassi DM (2021) Getting the ‘most out of the hotspot for practical conservation of groundwater biodiversity. *Global Ecology and Conservation* 31: e01844. <https://doi.org/10.1016/j.gecco.2021.e01844>

- Ilfie TM, Calderón-Gutiérrez F (2021) Bermuda's Walsingham Caves: A global hotspot for anchialine stygobionts. *Diversity* 13(8): 352. <https://doi.org/10.3390/d13080352>
- Jeannel R (1926) Faune cavernicole de la France avec une étude des conditions d'existence dans le domaine souterrain. Paul Lechevalier Editeur, 338 pp.
- Jeannel R (1943) Les fossiles vivants des cavernes. L'Avenir della Science, Nouvelle série no 1, Gallimard, Paris, 321 pp.
- Juberthie C, Decou V [Eds] (1994) Afrique. Encyclopaedia Biospeologica, Tome III, Société Internationale de Biospéologie, Moulis (France), Bucarest (Romania), 1461–1735.
- Karmaoui A, Ben Salem A, El Jaafari S, Chaachouay H, Moumane A, Hajji L (2022) Exploring the land use and land cover change in the period 2005–2020 in the province of Errachidia, the pre-Sahara of Morocco. *Frontiers in Earth Science* 10: 962097. <https://doi.org/10.3389/feart.2022.962097>
- Kayo RT, Marmonier P, Togouet SHZ, Nola M, Piscart C (2012) An annotated checklist of freshwater stygobiotic crustaceans of Africa and Madagascar. *Crustaceana* 85: 1613–1631. <https://doi.org/10.1163/15685403-00003134>
- Kováč Ľ (2018) Caves as Oligotrophic Ecosystems. In: Moldovan O, Kováč Ľ, Halse S (Eds) Cave Ecology. Ecological Studies, Vol. 235. Springer, Cham. [https://doi.org/10.1007/978-3-319-98852-8\\_13](https://doi.org/10.1007/978-3-319-98852-8_13)
- Labrique H (1995) Les *Scaurus* du groupe *tingitanus* Peyerimhoff (Coleoptera, Tenebrionidae). *Bulletin de la Société entomologique de France* 100(2): 119–126. <https://doi.org/10.3406/bsef.1995.17133>
- Magniez G (1978) *Magniezia gardei* n.sp. (Crustacea Isopoda Asellota): un Sténasellide des eaux souterraines du Maroc sud-oriental. *International Journal of Speleology* 9: 321–329. <https://doi.org/10.5038/1827-806X.9.3.9>
- Mammola S, Lunghi E, Bilandžija H, Cardoso P, Grimm V, Schmidt SI, Martínez A (2021) Collecting eco-evolutionary data in the dark: Impediments to subterranean research and how to overcome them. *Ecology and Evolution* 11(11): 5911–5926. <https://doi.org/10.1002/ece3.7556>
- Mascaro AL (1978) Un nuevo *Platyderus* de Marruecos (Coleoptera Pterostichidae). *Explorations* 2: 29–32.
- Maxwell SL, Cazalis V, Dudley N, Hoffmann M, Rodrigues ASL, Stolton S, Visconti P, Woodley S, Kingston N, Lewis E, Maron M, Strassburg BBN, Wenger A, Jonas HD, Venter O, Watson JEM (2020) Area-based conservation in the twenty-first century. *Nature* 586(7828): 217–227. <https://doi.org/10.1038/s41586-020-2773-z>
- Mendes-Rabelo L, Souza-Silva M, Ferreira RL (2018) Priority caves for biodiversity conservation in a key karst area of Brazil: comparing the applicability of cave conservation indices. *Biodiversity and Conservation* 27: 2097–2129. <https://doi.org/10.1007/s10531-018-1554-6>
- Mendes-Rabelo L, Souza-Silva M, Ferreira RL (2021) Epigean and hypogean drivers of Neotropical subterranean communities. *Journal of Biogeography* 48(3): 662–675. <https://doi.org/10.1111/jbi.14031>
- Messana G (2004) Africa: Bioespeleology. In: Gunn J (Eds) Encyclopedia of caves and karst science. Taylor & Francis, 48–51.

- Messouli M (2012) What can karstic organisms tell us about groundwater functioning and water quality? [https://balwois.com/wp-content/uploads/old\\_proc/ffp-636.pdf](https://balwois.com/wp-content/uploads/old_proc/ffp-636.pdf)
- Messouli M, Boutin C (2001) Past, Present and Future of Speleological Investigations in Morocco. 13<sup>th</sup> International Congress of Speleology 4<sup>th</sup> Speleological Congress of Latin America and Caribbean 26<sup>th</sup> Brazilian Congress of Speleology Brasília DF, 15–22. [https://doi.org/10.1007/978-3-540-85047-2\\_19](https://doi.org/10.1007/978-3-540-85047-2_19)
- Messouli M, Messana G, Yacoubi-Khebiza M, Filali AE, Ait Boughrous A, Boulanouar M (2008) The evolution of groundwater exploration methods in the Moroccan Oases through history and managing the ecological risk of their present pollution. Climatic Changes and Water Resources in the Middle East and North Africa, 267–288.
- MET [Ministère de l'Equipement et des Transports] (1981) Inventaire spéléologique du Maroc. Rabat.
- Monticelli Cardoso G, Du Preez G, Taiti S, Ferreira RL (2021) New troglobitic species of Niambia from Botswana and Namibia (Crustacea, Isopoda, Oniscidea). Subterranean Biology 40: 91–108. <https://doi.org/10.3897/subtbiol.40.72499>
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2020) Biodiversity hot-spots for conservation priorities. Nature 403: 853–858. <https://doi.org/10.1038/35002501>
- Nanni V, Piano E, Cardoso P, Isaia M, Mammola S (2023) An expert-based global assessment of threats and conservation measures for subterranean ecosystems. Biological Conservation 283: 110136. <https://doi.org/10.1016/j.biocon.2023.110136>
- Nehili A, Naouadir I (2021) Speleomedit Morocco. In: Maurano F, Didonna F (Eds) Speleomedit Méditerranean speleology Panoramic view of caves and karst of Mediterranean countries.
- Nicolosi G, Mammola S, Costanzo S, Sabella G, Cirrincione R, Signorello G, Isaia M (2021) Microhabitat selection of a Sicilian subterranean woodlouse and its implications for cave management. International Journal of Speleology 50(1): 53–63. <https://doi.org/10.5038/1827-806X.50.1.2370>
- Niemiller ML, Taylor SJ, Slay ME, Hobbs HH (2019) Biodiversity in the United States and Canada. In Encyclopedia of Caves, 163–176. [Academic Press] <https://doi.org/10.1016/B978-0-12-814124-3.00018-2>
- Niemiller ML, Taylor SJ, Bichuette ME (2018) Conservation of Cave Fauna, with an Emphasis on Europe and the Americas. In: Moldovan O, Kováč L, Halse S (Eds) Cave Ecology. Ecological Studies, Vol. 235. Springer, Cham, 451–478. [https://doi.org/10.1007/978-3-319-98852-8\\_22](https://doi.org/10.1007/978-3-319-98852-8_22)
- Novak T, Perc M, Lipovšek S, Janžekovič F (2012) Duality of terrestrial subterranean fauna. International Journal of Speleology 41(2): 181–88. <https://doi.org/10.5038/1827-806X.41.2.5>
- Ortuño VM, Gilgado JD, Jiménez-Valverde A, Sendra A, Pérez-Suárez G, Herrero-Borgoñón JJ (2013) The “aluvial mesovoid shallow substratum”, a new subterranean habitat. PLoS ONE 8(10): e76311. <https://doi.org/10.1371/journal.pone.0076311>
- Pacheco GSM, Souza Silva M, Cano E, Ferreira RL (2020) The role of microhabitats in structuring cave invertebrate communities in Guatemala. International Journal of Speleology 49(2): 161–169. <https://doi.org/10.5038/1827-806X.49.2.2333>

- Perreau PM, Faille A (2012) Contribution à la phylogénie et la systématique des Aleocharinae hypogés d'Afrique du Nord (Coleoptera: Staphylinidae). Annales de la Société entomologique de France 48(1–2): 81–96. <https://doi.org/10.1080/00379271.2012.10697755>
- Pipan T, Deharveng L, Culver DC (2020) Hotspots of subterranean biodiversity. Diversity 12(5): 209. <https://doi.org/10.3390/d12050209>
- Pipan T, Blejec A, Brancelj A (2006) Multivariate analysis of copepod assemblages in epikarstic waters of some Slovenian caves. Hydrobiologia 559: 213–223. <https://doi.org/10.1007/s10750-005-0920-z>
- Pipan T (2004) Epikarst—a promising habitat. In: Batelaan O, Dusar M, Masschelein J, Tam VT, Van TT, Khien NX (Eds) Trans-KARST 2004, Proceedings of the International Trans-disciplinary Conference on Development and Conservation of Karst Regions, Hanoi, Vietnam, 176–178.
- Sánchez-Fernández D, Galassi D M, Wynne JJ, Cardoso P, Mammola S (2021) Don't forget subterranean ecosystems in climate change agendas. Nature Climate Change 11(6): 458–459. <https://doi.org/10.1038/s41558-021-01057-y>
- Sket B (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42: 1549–1563. <https://doi.org/10.1080/00222930801995762>
- Sket B, Paragamian K, Trontelj P (2004) A census of the obligate subterranean fauna of the Balkan Peninsula. In Balkan Biodiversity: pattern and process in the European hotspot. Dordrecht: Springer Netherlands, 309–322. [https://doi.org/10.1007/978-1-4020-2854-0\\_18](https://doi.org/10.1007/978-1-4020-2854-0_18)
- Sousa Barros J, Bernard E, Ferreira RL (2021) An exceptionally high bat species richness in a cave conservation hotspot in Central Brazil. Acta Chiropterologica 23(1): 233–245. <https://doi.org/10.3161/15081109ACC2021.23.1.020>
- Souza MFVR, Ferreira RL (2022) Two extraordinary troglobitic species of *Allokoenenia* (Eukoeneniidae: Palpigradi) from Brazil: first records of this initially monotypic genus more than a century after its Description. European Journal of Taxonomy 789: 11–48. <https://doi.org/10.5852/ejt.2022.789.1627>
- Souza-Silva M, Ferreira RL, Gonçalves LV (2019) Public support as a key element for fauna conservation in Maquiné and Rei do Mato show caves. Espeleo-Tema 29: 65–76.
- Souza-Silva M, Cerqueira RFV, Pellegrini TG, Ferreira RL (2021) Habitat selection of cave-restricted fauna in a new hotspot of subterranean biodiversity in Neotropics. Biodiversity and Conservation 30(14): 4223–4250. <https://doi.org/10.1007/s10531-021-02302-8>
- Souza Silva M, Martins RP, Ferreira RL (2015) Cave conservation priority index to adopt a rapid protection strategy: a case study in Brazilian Atlantic rain forest. Environmental Management 55: 279–295. <https://doi.org/10.1007/s00267-014-0414-8>
- Souza-Silva M, Ferreira RL (2016) The first two hotspots of subterranean biodiversity in South America. Subterranean Biology 19: 1–21.
- Strinati P, Aellen V (1959) Faune cavernicole de la région de Taza (Maroc), Revue suisse de zoologie 4(66): 765–777. <https://doi.org/10.5962/bhl.part.75227>
- Stüben PE (2009) Neubeschreibungen westpaläarktischer Crytorhynchinae III (*Torneuma*, *Echinodera*, *Acalles*). Snudebiller 10: 94–106.

- Trontelj P, Blejec A, Fišer C (2012) Ecomorphological convergence of cave communities. *Evolution* 66(12): 3852–3865. <https://doi.org/10.1111/j.1558-5646.2012.01734.x>
- Togouet SHZ, Boutin C, Njiné T, Kemka N, Nola M, Menbohan SF (2009) First data on the groundwater quality and aquatic fauna of some wells and springs from Yaounde (Cameroon). *European Journal of water quality* 40(1): 51–74. <https://doi.org/10.1051/water/2009005>
- Urich PB, Day MJ, Lynagh F (2001) Policy and practice in karst landscape protection: 26 Bohol, the Philippines. *Geographical Journal* 167: 305–323. <https://doi.org/10.1111/1475-4959.00028>
- Vandel A (2013) Biospeleology: the biology of cavernicolous animals (Vol. 22). Elsevier, 524 pages. Translated into English by B. E. Freeman. This is an authorized translation of the original volume Biospéologie - la biologie des animaux cavernicoles published in 1964 by Gauthier-Villars, Paris.
- Viñolas A, Masó G (2005) *Hadrobregmus bicolor* Español, 1988, designació de lectotipus. *Butletí de la Institució Catalana d'Història Natural* 73: 125–126.
- Wilkens H, Culver DC, Humphreys WF (2000) Subterranean ecosystems. Amsterdam: Elsevier.
- Wynne JJ, Howarth FG, Sommer S, Dickson BG (2019) Fifty years of cave arthropod sampling: Techniques and best practices. *International Journal of Speleology* 48(1): 33–48. <https://doi.org/10.5038/1827-806X.48.1.2231>
- Zagmajster M, Malard F, Eme D, Culver DC (2018) Subterranean Biodiversity Patterns from Global to Regional Scales. In: Moldovan O, Kováč L, Halse S (Eds) *Cave Ecology. Ecological Studies*, Vol. 235. Springer, Cham. [https://doi.org/10.1007/978-3-319-98852-8\\_9](https://doi.org/10.1007/978-3-319-98852-8_9)